

and Sons, Riverside, California. Barry Prigge and Christopher Davidson assisted in quantitative studies. Frances Runyan provided the illustration.

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PRIMARY SUCCESSION ON GRANITE OUTCROPS IN THE MONTANE SOUTHERN SIERRA NEVADA

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Although primary succession has been widely studied, little attention has been given to its occurrence in the mountains of the western United States, despite the extensive distribution of rock outcrops. On the west slope of the Sierra Nevada, 29 percent of the total area above 1,543 m (5,000 ft) consists of rock or bare ground surfaces (Richards, 1959). This paper reports on general patterns of primary succession present on granite outcrops in the montane zone of the southern Sierra Nevada of California, including colonization by both cryptogams and vascular plants.

Much of the ecological literature on primary succession on rock surfaces (e.g., Cooper, 1913; Oosting and Anderson, 1937; Lawrence, 1958) have implied that primary succession progresses linearly from colonization by cryptogams, through herbaceous and shrub communities to an eventual climax forest community. Each later stage is dependent on physical and biotic changes brought about by the earlier stage. Recent studies in Hawaii on lava rock, however, have shown that a different progression can occur (Atkinson, 1970). *Metrosideros collina* (ohia) is the dominant climax forest species on incipiently weathered lava and is also one of the first colonizers on sterile outcrops. While cryptogamic communities may become established more rapidly, they have little significance in the establishment of *Metrosideros* seedlings within crevices on the lava outcrops.

Primary succession on granite outcrops in the montane southern Sierra Nevada shows a pattern similar to that described for *Metrosideros* in Hawaii. Climax woody species appear early in the successful development of the outcrops, with little influence of cryptogamic or herbaceous com-

munities. While lichens and bryophytes comprise the earliest colonizers on granite outcrops, succession on these outcrops is primarily a function of physiographic weathering leading to the formation of fracture lines suitable for colonization by woody plants. Although environmental modifications brought about by bryophyte communities may lead to outcrop colonization by vascular plants, this situation is rarely important in the overall succession toward climax communities. In describing the general nature and patterns of primary colonization and succession as they occur on granite outcrops in the montane zone of the southern Sierra Nevada, this paper includes a broad discussion of both the nature of early outcrop colonization by lichens and mosses and the relationship of vascular plant colonization to crevice formation and soil development on outcrop surfaces.

MATERIALS AND METHODS

A series of granite outcrops between 1900 and 2100 m was studied extensively in Sequoia National Park and Sequoia National Forest. Detailed analysis and physiological measurements were carried out on a southwest-facing outcrop 0.5 km west of Crescent Meadow, Giant Forest, Sequoia National Park.

Analyses of soil chemistry were made by the Soil Testing Division, North Carolina State University, Raleigh. Methods of determination were as follows: pH-glass electrode; organic matter— $\text{H}_2\text{SO}_4\text{-Na}_2\text{Cr}_2\text{O}_7$; and Ca, P, K, NH— $\text{HCl-H}_2\text{SO}_4$ extract. Water potential measurements were made with a Scholander-type pressure bomb. Details of the methods of pressure bomb measurements have been previously described (Rundel, 1972). Growth increment measurements of tree cores were made with a dissecting microscope utilizing a dendrometer constructed from a threaded mounting stage and Ames dial micrometer.

I thank William A. Weber for assistance in the identification of lichen species and Richard Zander for identification of bryophytes. Lichen nomenclature follows that of Hale and Culberson (1970), bryophytes that of Crum et al. (1973). Vascular plant nomenclature follows Munz (1959).

GENERAL PATTERN OF SUCCESSION

General patterns of outcrop succession are shown in Figure 1. Smooth granite outcrops provide a poor substrate for vascular plant growth; therefore primary colonizers are restricted to lichens and bryophytes. Although environmental modifications brought about by certain bryophytes may lead to outcrop colonization by vascular plants, this situation is unimportant in the overall succession toward climax communities. Only rarely are vascular plants able to colonize an outcrop before physiographic weathering has produced suitable habitats in the form of fracture lines. A variety of herbaceous perennials and woody species are able to colonize crevices with sand accumulation and adequate moisture

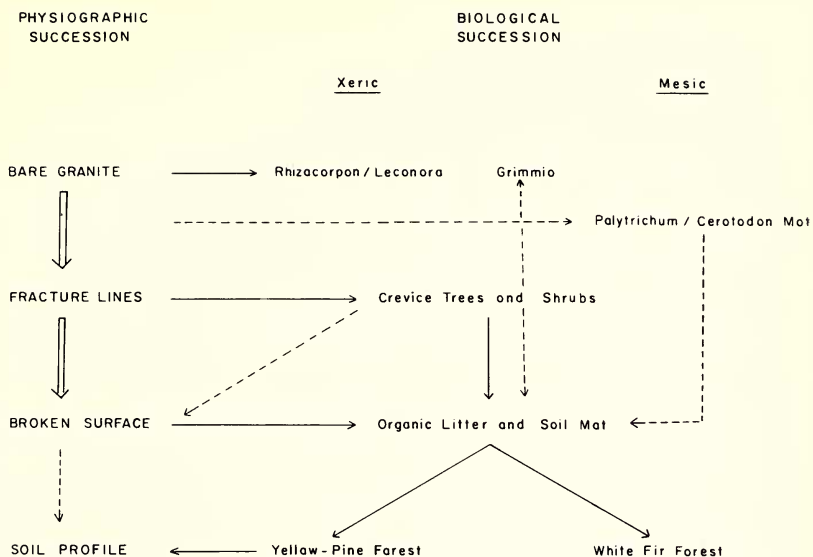


FIG. 1. Primary succession on granite outcrops in the montane southern Sierra Nevada.

conditions. Even individuals of climax coniferous tree species may become colonizers at this stage.

For biological succession to progress from crevice plant colonizers to a climax coniferous forest, it is necessary to develop an organic soil mat. There are two means by which such soil mats may develop. Without question the most important process by which soil mat formation takes place is the in situ formation of soils on broken outcrop surfaces in the most developed stage of physiographic succession. With repeated fracturing of horizontal granite outcrops, aided by winter freeze-thaw cycles, the surface of the outcrop is eventually broken into an irregular accumulation of angular rocks and boulders. The time necessary to produce such a broken surface by physiographic succession is extremely variable, depending on the structural relationships of individual outcrops. Once a broken outcrop surface exists, soil formation can proceed at a steadily accelerating pace. Of lesser importance overall is soil mat formation from litter accumulation around the bases of colonizing trees and shrubs in crevice habitats. Under stable conditions, an increasingly well-developed organic soil mat expands outward as litter fall continues.

BIOLOGICAL SUCCESSION

Colonization by Lichens. Two species of crustose lichens, *Rhizocarpon bolanderi* and *Lecanora gibbosa*, overwhelmingly dominate the earliest stages of succession on montane granite outcrops in the southern Sierra

Nevada. The majority of the exposed granite surfaces of the outcrops are covered by these two species, in particular the former. Only in areas of rapidly exfoliating rock surface or in channels subject to the abrasive action of runoff from snow melt and precipitation are these species absent.

Few other species of lichens occur with any regularity on the exposed horizontal surfaces of these outcrops. *Dermatocarpon miniatum* and *Candelariella* sp. occur irregularly on the outcrops but never with large coverage. The great majority of saxicolous species on the outcrops occur on sites with reduced levels of solar radiation, such as vertical rock faces or on the sides of loose granite boulders. *Rhizocarpon geographicum*, *Lecidea* spp., *Umbilicaria phaea*, and *Parmelia conspersa* are typical associates in these habitats.

Colonization by Bryophytes. Despite the abundance of crustose lichens on the granite outcrops, these species contribute little if any to the succession toward more advanced plant communities. Another early colonizer on the outcrop surface, *Grimmia unicolor*, is far more important in biological succession.

Conditions for the establishment of *Grimmia unicolor* on the outcrops are ideal during the late spring in the Sierra Nevada. The necessary conditions for successful vegetative establishment of *Grimmia laevigata* on granite outcrops were described by Keever (1957) as follows: 1) wetting of a fragment of a *Grimmia* gametophyte by heavy dew or rain every 4–5 days for at least 2–3 weeks; 2) cloudy, cool but not freezing weather; and 3) subsequent dry, sunny weather. Conditions present on granite outcrops during spring snow melt in the Sierra Nevada provide this sequence of events. Vegetative growth is accomplished through the spread of protonema. Once established, these protonema are extremely drought resistant, and they may survive a month or more without any addition of water. Mature gametophytes of *Grimmia laevigata* are known to remain viable for ten years or more in herbaria (Keever, 1957).

The distribution of *Grimmia unicolor* on the granite outcrops is strongly related to the microtopography of the outcrop. In most instances the occurrence of *Grimmia* is correlated with minute rough places in the granite surface where the gametophytes have been able to form a strong attachment. *Grimmia* is most common on the granite outcrops along the margins of drainage channels. *Grimmia* is absent from the bottoms of these channels, apparently kept out by the abrasive action of water and sand during spring runoff; it is almost always present along the margins of these channels. The microtopography of channel margins provides a roughened surface to trap fragments of *Grimmia*, which are kept moist in the early stages of their establishment by water from spring snow melt moving along the drainage channel.

Although small *Grimmia* mats may trap significant amounts of weathered granite soil (up to 10 mm in depth), the irregular presence of these small mats makes them of minimal importance in biological succession

leading to communities of vascular plants. Rarely, *Grimmia* is found along the margins of organic litter mats, indicating that *Grimmia* is of some value in extending margins of mats. Establishment of these *Grimmia* populations, however, undoubtedly postdates the formation of the litter mat, as indicated by restriction of these populations to the down-slope margins of mats. Seepage of water trapped by mats provides ideal conditions for establishment of *Grimmia*.

Seepage zones and channels on granite outcrops commonly produce a more mesic development of bryophyte colonization. The most widespread community of this seepage zone succession is the *Polytrichum juniperinum*-*Ceratodon purpureus* mat. Small to moderately-sized mats of discontinuous distribution form along areas where seepage flows during periods of precipitation or snow melt.

Small, discontinuous *Polytrichum-Ceratodon* mats are common in areas of shallow soil accumulation on broken granite surfaces. In almost all cases, these mats are associated with what appear to be runoff channels, collecting water in times of precipitation from other parts of the outcrop. Where drainage channels are well-defined, the mats may be restricted to margins of channels. Generally, the center of these well-defined channels are bare of soil or any lichens or bryophytes. In certain instances, however, thick mats of *Racomitrium fasciculare* may cover the smooth surface of the channel. Soil accumulation in such mats reaches 5 cm. Major drainage channels along outcrops often show a gradation from thick mats of *Racomitrium fasciculare* in the center of the channel to an irregular band of *Polytrichum-Ceratodon* mat along the inner margin of the channel. *Grimmia unicolor* occurs along the outer margins of these channels.

On relatively steep granite slopes of 20–30° or more, pure mats of *Ceratodon purpureus* are common where springs or late snow melt provide a continuously wet rock surface well into the summer months. Soil accumulation reaches 5 cm or more within these mats. If water supply is adequate, the mats will support growth of a variety of annual vascular plants. Mats of *Bryum* or *Tortula ruralis* in similar situations may also support herb growth, typically *Linanthus montanus*. Such occurrences of herbaceous species growing from the soil accumulated within moss mats, however, are rare.

Although a number of species of bryophytes are common primary colonizers on granite outcrops in the southern Sierra Nevada, it is rare that they play a significant role in biological succession leading to establishment of vascular plant species on the outcrops. In no instance has primary succession by *Grimmia bicolor* been observed to lead to establishment of higher plants. Where vegetation mats have been formed as a result of other conditions, as described later in this paper, *Grimmia* may occasionally play a small part in increasing the outer margin of an outcrop by accumulation of soil debris. Thick mats of moss in seepage zones may build soil mats to 5 cm in depth but this soil accumulation

rarely, if ever, leads to establishment of a more advanced stage of succession.

Crevice Succession. As physiographic succession proceeds from bare granite to the formation of fracture lines across the surface, vascular plants are able to colonize outcrops. On the majority of outcrops, fracture line crevices are a prominent feature. Typically these fracture lines average 2–5 cm in width and may extend for 20 m or more across the outcrop. Wind-blown sands and organic matter collect within these crevices.

On most montane outcrops in the southern Sierra Nevada, *Zauschneria californica* ssp. *latifolia* is the primary vascular plant colonizer of the crevice habitat. Even along fracture lines where soil accumulation within crevices is essentially absent, *Zauschneria* is commonly found. Often it is the only vascular plant present over large portions of outcrops. Second in importance is *Lomatium torreyi*, endemic to the central and southern Sierra Nevada. Although not as frequent as *Zauschneria*, *L. torreyi* often shows greater densities on individual outcrops. Both species are characterized by thick, woody taproots, possibly a morphological adaptation for water and carbohydrate storage. Four other species are also characteristic of this crevice community. *Calyptridium umbellatum*, while not restricted to this habitat, is common along fracture lines on outcrops. *Hieracium horridum*, *Streptanthus tortuosus*, and *Eriogonum wrightii* var. *subscaposum* may be locally important, but none of these species was present on a majority of outcrops studied.

Crevices beneath ledges or shaded by large boulders often include one or more species of ferns: *Pellaea bridgesii*, *Onychium densum*, and *Cheilanthes gracillima*. *Zauschneria californica* var. *latifolia* is again present. The moisture relations of these sites must be more favorable than along more exposed fracture lines, for these same species occur in rocky areas where seepage from snowmelt and spring rains continues into summer.

Establishment of Woody Plants. The establishment of woody plants is the most significant stage in colonization of granite outcrops leading to the development of soil cover. During years of favorable conditions, seeds of a number of tree and shrub species germinate and establish seedlings in soil within crevices. *Pinus jeffreyi*, *Libocedrus decurrens*, and *Arctostaphylos patula* occur frequently as primary colonizers on outcrops studied. Less frequently, a number of other trees and shrubs may act as primary colonizers. These include (in order of decreasing frequency of occurrence) *Pinus ponderosa* (below 1800 m), *Quercus kelloggii*, *Quercus chrysolepis*, *Arctostaphylos viscida* (below 1800 m), *Abies concolor*, and *Ceanothus cordulatus*. There is no evidence that the establishment of any of these species requires any previous biological succession on an outcrop. Given minimal levels of available moisture, windblown sand and trapped soil particles provide sufficient conditions for seedling establishment. A number of characteristically mesic species are also occasion-

ally found as primary colonizers, including *Corylus rostrata*, *Rubus parviflorus*, and *Sequoiadendron giganteum*.

The typical pattern of establishment of woody colonizers in crevice microhabitats consists of a period of years of slow growth while root systems become established, followed by more rapid growth when the root system is able to tap a reliable source of underground water. This pattern is illustrated in Figure 2 for two *Libocedrus decurrens* growing in crevice habitats on an outcrop near Crescent Meadow (Sequoia National Park). Both of these trees are stunted. Tree 1 shows a slow but increasing annual increment of growth over its first 25 years. From that point, it has shown a mean annual growth increment of about 1.5 mm, oscillating in relation to annual precipitation. Tree 2 likewise showed a slow relative growth rate for its first 25 years, followed by a rapid increase to a mean annual growth increment of approximately 2.5 mm.

The observed growth response of these two trees correlated well with patterns of water stress measured during the summer of 1968. Tree 1 with a mean annual growth increment of 1.0 to 1.5 mm had a maximum midday xylem pressure potential (shaded branch) of -27.2 bars in mid-summer. It produced no cones in 1968. Tree 2, with a sparse cone crop, had a lower maximum stress of -25.7 bars. Individuals of *L. decurrens* with similar diameters (dbh) but normal height and heavy cone crop, growing on shallow soils nearby had a maximum stress of -18 bars. This maximum stress occurred relatively late in summer, allowing a much longer growing season than for the two outcrop trees. Restricted growing seasons for the outcrop trees is apparently reflected in a lack of available carbohydrate reserves for normal height growth and production of cone crops.

Formation of Soil Mats. Although vascular plants are first able to colonize granite outcrops during the fracture line stage of physiographic succession, few species successfully develop in these specialized crevice habitats. Diversity of the outcrop community can increase only following formation of a suitable soil substrate for germination and establishment of a larger flora of annual and perennial species. Such a soil substrate may develop either by the action of physiographic succession on the outcrop or by biological succession acting through accumulation of litter under crevice shrubs and trees.

In the first stages of physiographic succession on broken outcrop surfaces, vascular plants occur infrequently. Jumbled, angular rocks dominate the outcrop surface. Sands and gravels are primarily restricted to crevices, although wind-blown sediments may collect behind sheltered rocks or in vernal pools on the outcrop. Vascular plants are limited to crevice habitats, as previously described. As physiographic succession continues, accumulations of granite sand develop, forming an irregular layer 1 cm or more in depth. Little or no organic matter is present and vascular plants are rare or absent. The dominant perennials *Calyptidium umbellatum*, *Streptanthus tortuosus*, *Eriogonum wrightii* var. *subscapo-*

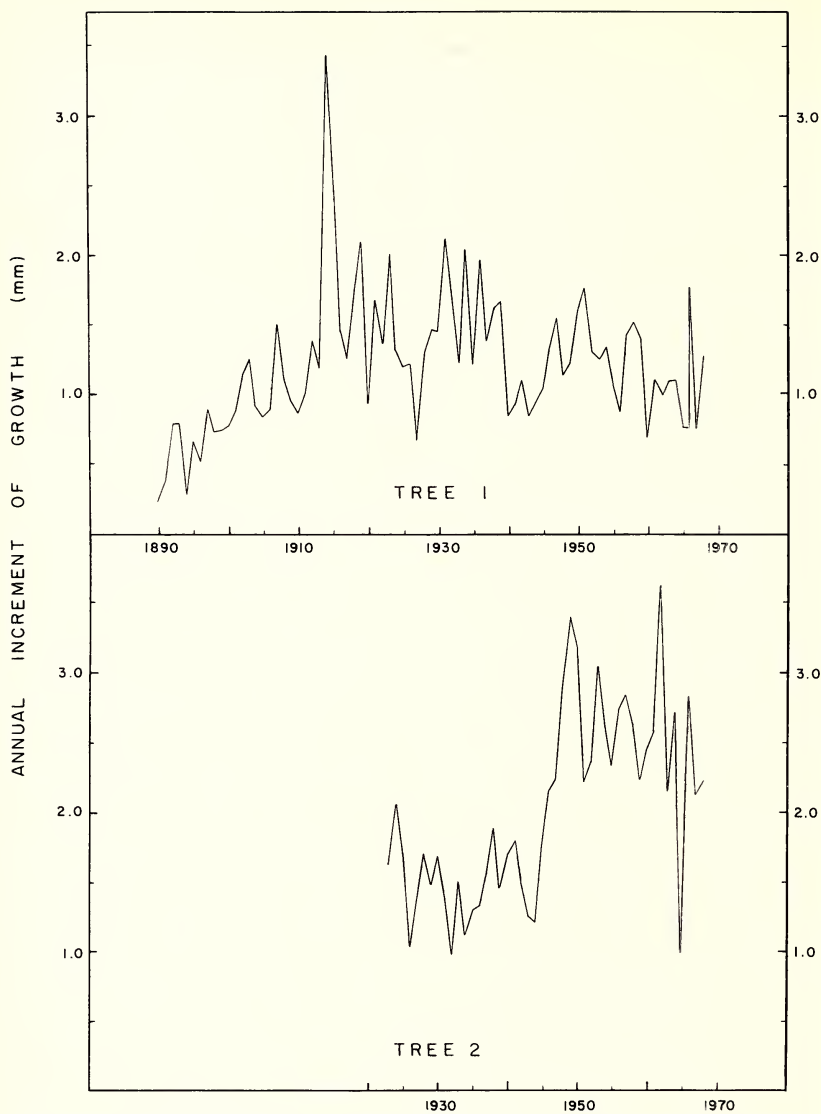


FIG. 2. Annual increment of growth for two *Libocedrus decurrens* growing in crevice habitats on a granite outcrop at 2040 m near Crescent Meadow (Giant Forest), Sequoia National Park.

sum, and *Lomatium torreyi* are joined by *Eriogonum nudum*, *Polytrichum juniperinum*, and *Ceratodon purpureus*. Basal rosettes of *Calyptidium umbellatum* and *Eriogonum nudum* are particularly frequent.

Diversity of outcrop communities increases rapidly as continued weathering processes produce relatively continuous granitic sands, richer in

finer sands, particles, silt, and organic matter. Outcrop surfaces with 2–5 cm of granitic soil are characterized by relatively rich carpets of spring annuals.

Linanthus montanus may carpet almost every square centimeter of the thin soil on outcrops. Locally, *Phacelia orogenes* and *Eriogonum spergulinum* may be abundant. A number of perennial species are also of importance: *Calyptidium umbellatum*, *Pteryxia terebinthina* var. *californica*, *Lotus nevadensis*, and *Perideridia gairdneri*. With the formation of distinctive soil profiles, 5–15 cm or more in depth and rich in organic matter, these species are replaced or overshadowed by a group of herbaceous species characteristic of xerophytic communities within yellow pine forests, e.g., *Pedicularis semibarbatus*, *Viola purpurea*, *Allophyllum integrifolium*, *Gayophytum nuttallii*, *Horkelia tridentata*, *Cryptantha affine*, and *Stipa* spp. These species are also common in open areas in the *Pinus ponderosa* (*P. jeffreyi*)/*Arctostaphylos* community on more developed sites. Climax species of trees and shrubs begin to colonize outcrop surfaces at this stage without reliance on crevices.

Biologically induced succession through the accumulation of organic litter in mats beneath crevice trees and shrubs on outcrops may also lead to development of significant soil substrates on outcrops. Organic debris is the most important element in early development of these litter mats. Granitic sands, important in the physiographic formation of outcrop soils, do not build up to significant depths until an organic substrate accumulates to trap them. Litter mats 5–10 cm in depth are common beneath isolated, crevice-growing individuals of *Arctostaphylos patula* and *Pinus jeffreyi*. Where hollows on the outcrop shelter the rock surface beneath crevice trees and shrubs, the accumulation of organic debris (and trapped inorganic sands) may be considerably greater. As organic litter accumulation exceeds a few centimeters in depth, herbaceous species colonize the soil mat. In almost all cases, these species are identical with those typical of the latter two stages.

Although chemical changes associated with soil development on granite outcrops have not been studied in detail, some idea of the changes involved can be seen in results of a transect made across an outcrop near Crescent Meadow, where soils were sampled at varying stages of successional development from primary moss colonizers to mature forest. Soil samples were collected from debris beneath thalli of *Grimmia unicolor*, the primary bryophyte colonizer on bare outcrop surfaces. A second series of samples was collected beneath mats of *Polytrichum juniperinum*, where 1–2 cm or more of soil was often present. Finally, samples were collected at two sites supporting coniferous trees: shallow soil mats (20–50 cm) at the outcrop edge with *Abies concolor* and *Libocedrus decurrens*; deeper soils (40–90 cm) at the margin of a grove of *Sequoiadendron giganteum*. Changes in soil chemistry determined along this gradient are shown in Figure 3.

Soil pH changed steadily with succession from 4.4 beneath *Grimmia*

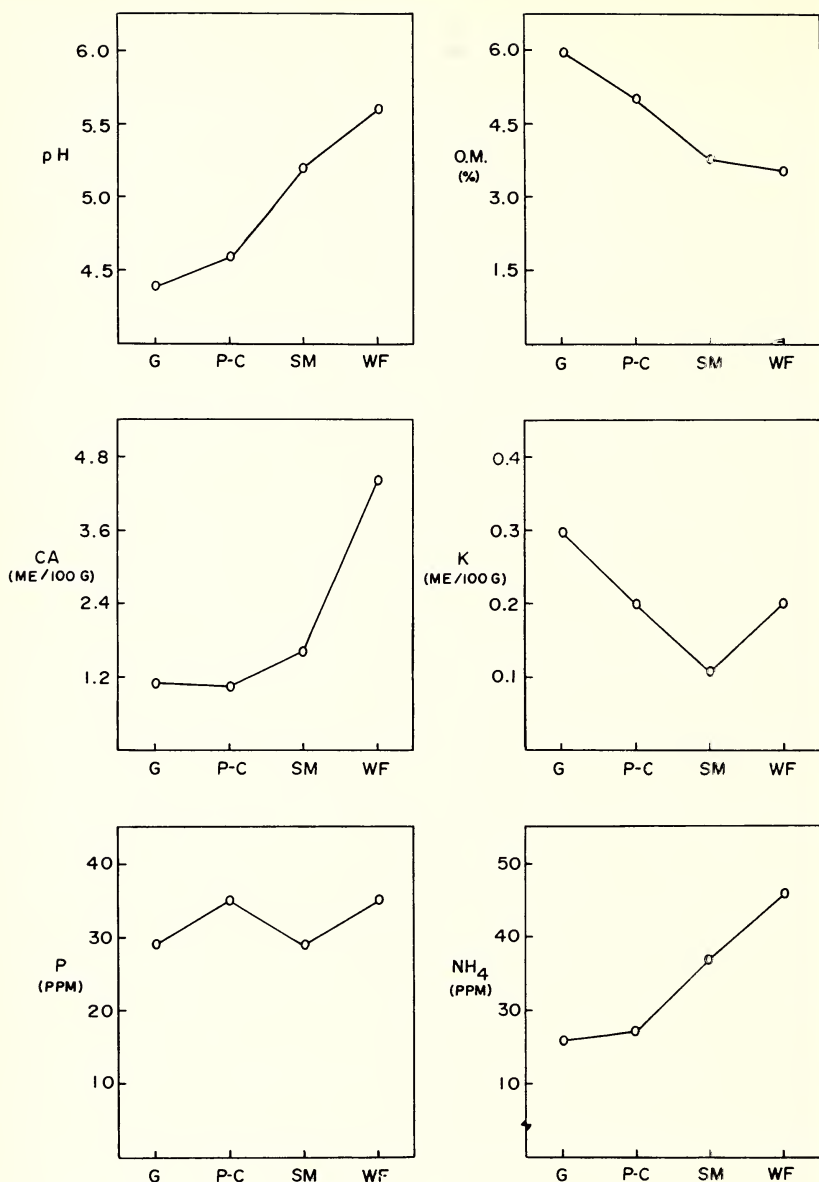


FIG. 3. Gradient of soil chemical characteristics (pH, organic matter, Ca, K, P, NH₄) across a granite outcrop at 2040 m near Crescent Meadow (Giant Forest), Sequoia National Park. G = *Grimmia* stage, P-C = *Polytrichum-Ceratodon* mat, SM = soil mat at edge of white fir forest (20–50 cm soil profile), WF = white fir forest with 40–90 cm soil profile.

to 5.6 in soils associated with *Sequoiadendron*. Organic matter content, highest beneath the moss mats due to litter from the thalli above, was relatively consistent between 3.5 and 3.6 percent under the coniferous canopy. This low level indicates the extremely slow accumulation of organic matter in these soils. Both Ca and NH₄ show steady increases with greater soil development, while K appears to become slightly reduced in concentration. Major changes in P concentration were not observed.

Climax Vegetation. Climax vegetation in montane southern Sierra Nevada consists of a coniferous forest of variable composition. Differential fire history has produced a mosaic of forest stands differing in structure and species importance. The role of fire in successional sequences in the Sierra Nevada is beyond the scope of this paper. Many papers discuss this subject in detail (Show and Kotok, 1924; Rundel, 1971; Vankat, 1970; Kilgore, 1973).

Mesic facies of mature forest communities in the study area are strongly dominated by *Abies concolor*. *Pinus lambertiana* is a constant associate, and *Libocedrus decurrens* may be important, particularly below 1880 m. *Sequoiadendron giganteum* is an important associate locally in areas with abundant ground water. Characteristic understory species include *Corylus rostrata*, *Cornus nuttallii*, *Pteridium aquilinum* var. *lanuginosum*, and *Rubus parviflorus*. Xeric facies of mature forest communities can best be designated as yellow pine forest. The dominant tree species are *Pinus jeffreyi* and *P. ponderosa*, with *Libocedrus decurrens* and *Quercus kelloggii* as regular associates. Characteristic understory species are *Chamaebatia foliolosa*, *Arctostaphylos patula*, *A. viscida* (below 1800 m), *Ceanothus integerrimus*, and *Ribes roezlii*.

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PROSOPIS PALMERI: A RELICT OF AN ANCIENT NORTH AMERICAN COLONIZATION

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Baja California has long been recognized as the home of many endemic and often bizarre plant taxa (Shreve and Wiggins, 1964; Humphrey, 1970). Even the genus *Prosopis* (Leguminosae, Mimosoideae), usually thought of in terms of commonplace mesquites and screwbeans, has a singular representative, *P. palmeri* S. Wats., restricted to the lower Sonoran Zone (Shreve and Wiggins, 1964). Because of its confusing characters and scarcity in collections, this taxon has been placed in various sections of *Prosopis* (Watson, 1889; Burkart, 1940; Schuster, 1969) or in a monotypic genus *Sopropis* (Britton and Rose, 1928). The most recent treatment of the Leguminosae by Hutchinson (1964) returned *P. palmeri* to a monotypic genus. We report here results of an overall study of *Prosopis* (Carman, 1973; Burkart, in press) that indicate *P. palmeri* should not only be retained in *Prosopis* but should also be placed in a section to which it has not previously been referred. In addition, our study of *P. palmeri* helps to confirm a decision to unite two former sections of the genus (Burkart, in press) and provides clues for the evolutionary history of *Prosopis*.

In a current revision of *Prosopis*, Burkart (in press) has separated the genus into five sections based on the morphological characters shown in Table 1. The largest section, *Algarobia*, contains the 29 species known as mesquites in North America and algarrobos in South America. The second largest section, *Strombocarpa*, formerly contained only the screwbeans (Burkart, 1940) but has been modified to include the two species

† Deceased